

# Pelagic Food Webs of the East African Great Lakes

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**Abstract** — The pelagic food webs of the East African Great Lakes exhibit features that suggest continuous, strong biological interactions as well as strong interactions between biota and their geochemical environment. Planktivory by both vertebrate and invertebrate predators appears to be a major structuring force affecting the animal communities. The phytoplankton appear to control or modify nutrient chemical conditions during an “endless summer” of strong interactions with resource levels. Several case studies illustrate the roles of these interactions in food web processes. The Dipteran larva *Chaoborus* appears to be an important predator whose distribution may be controlled by interactions between fish planktivory and the availability of oxygenated refugia. The strength of biological interactions is supported not only by the patterns of extant distributions among African Great Lakes, but also by the food web changes observed when efficient planktivorous fish are introduced into lakes. Lake Victoria is given special attention as a lake that has exhibited changes in limnological condition during the present century which seem to be driven primarily by changes in nutrient income and regional climate. The neolimnological changes in the lake are associated with conditions that leave interpretable signals in the stratigraphic record of the lake sediments. Thus Victoria represents a candidate lake for calibration of the tools and models that will be needed to infer past climate variations and ecosystem changes in other East African lakes.

The Great Lakes of East Africa are remarkable for their immense biological diversity. Some faunal elements, particularly fish and mollusks, have developed species richnesses that are of great scientific value for the study of speciation, extinction, and ecological interactions. One striking enigma of the African Great Lakes, however, is the contrast between levels of biodiversity in their littoral and benthic habitats with those of the lake pelagia. Most of the species richness in these lakes is confined to nearshore regions, and biological communities in offshore areas may be species-poor in comparison with some temperate Great Lakes ecosystems.

The purpose of this effort is to review existing information about the pelagic food webs of the East African Great Lakes, to identify generalizations, and to develop hypotheses about the open lake ecosystems. The analysis cannot be entirely satisfactory because the quantitative data necessary to compare and contrast the lakes are rarely available and are in no case complete. Nonetheless, these lakes present tantalizing patterns that are expressed in the form of ecological associations from basin to basin, and in the consistency of biological changes along spatial gradients. There is reason for optimism that careful study of the pelagic environments will reward us with rather precise information about the conditions that promote the success of alternative food webs, and thereby will give us a reliable way to interrogate the high resolution ecological and environmental stories recorded in the African lake sediments.

Present understanding of the African lakes points to a set of influential factors that affect pelagic food webs. First, even though the lakes are subject to seasonal variations in heat and water balance, and also to drainage basin and nutrient income effects, those external influences are less profound for these tropical great lakes than the external influences of seasonality that affect temperate great lakes. Kilham and Kilham (1990) have argued that the "endless summer" of tropical lakes permits biological control of elemental cycles to adjust to the nutrient regime fully, whereas temperate lakes are constrained by a physical environment that dominates seasonally and forcibly resets the biological system with hostile conditions of cold temperature and low light. Consequently, in the African Great Lakes the biota can interact with and alter their nutrient and chemical environment year-round, whereas for most of the year, temperate lake communities can only experience and adapt to their environment.

Prominence of biological forces in the tropical lakes does not mean that physical forces are unimportant or even of secondary importance. Physical influences promote important biological responses in African Great Lakes. Talling (1969) and Hecky and Kling (1987) have emphasized the importance of vertical stratification and mixing depth of the rift lakes as the major controlling variable for phytoplankton species composition, community changes, and perhaps biomass levels as well. Deep mixing and upwelling processes (Hecky et al. 1991) not only inject nutrient stores from hypolimnetic or monimolimnetic reservoirs into the surface water, but they subject algal cells to variable light regimes which favor taxa that can exploit the conditions. Changes in taxonomic representation among the algae cause feedbacks to the lake nutrient regimes, expressed through uptake of silica by diatoms, for example, or through active nitrogen fixation by diazotrophic cyanobacteria. The long-term consistency of most African Great Lakes phytoplankton communities, inferred from the presence of diatoms which leave stratigraphic records, argues that far from being haphazard assemblages of taxa, the lake communities are crafted by master controlling influences that are reproducible over sometimes thousands of years of record (Hecky 1984b).

The bulk of the phytoplankton biomass in the African Great Lakes is dominated by relatively few, widespread taxa mainly drawn from the green algae, diatoms, and cyanobacteria. This tendency toward parsimony is even greater in the offshore zooplankton communities of these lakes. The crustacean plankton is much simpler than in temperate lakes (Fernando 1980a, 1980b; Lehman 1988) and the pelagic is not rich in rotifers, either (see below). In Lake Tanganyika, ciliate protozoa account for a substantial fraction of the plankton biomass at times (Hecky and Kling 1981), but the dominant ciliate during stable stratification, *Strombidium*, contains endosymbiotic zoochlorellae, and is thus potentially an autotroph.

Quantitative comparisons of plankton biomass and relative composition among the lakes are extremely difficult owing first to the scarcity of relevant studies and second to the extreme differences in collection methods and mesh sizes of nets employed. The pioneering studies of Worthington (Worthington 1931; Worthington and Ricardo 1936), for instance, provide useful data on the vertical distributions of some planktonic species, but the nets used were most suitable for sampling oceanic calanoid copepods with such large mesh that most life stages of the abundant cyclopoid copepods that now dominate the lake plankton would have been missed. Similarly, biomass values for Lake Tanganyika based on collections with 300  $\mu\text{m}$  and 400  $\mu\text{m}$  mesh apertures (Burgis 1984) must be suspected of underestimating the zooplankton. In view of the probability that many herbivorous crustacean plankton were missed in the sampling, it is especially noteworthy that Burgis' estimates demonstrate that

zooplankton biomass exceeds algal biomass in Lake Tanganyika (Hecky 1991), which in turn suggests the potential for grazer control of the algae through much of the year.

Offshore copepod assemblages of the African Great Lakes are typically represented by a single dominant diaptomid species (although *Diaptomus* has been reported to be missing from Lake Albert, see below), and one or more common cyclopoid species, usually including the predator *Mesocyclops*. The Cladocera are represented typically by two or more species, and the size structure of the community varies between inshore and offshore sites (Green 1967a, 1971). Based on historical reports, the Cladocera and Cyclopoida are usually more diverse inshore than offshore, and in the extreme case of Lake Tanganyika, the Cladocera are entirely absent. Meroplanktonic representatives include species of the planktivorous lake fly *Chaoborus* and atyid prawns (e.g., *Caridina*).

For reasons that will be explained in the following pages, the compositional features of the zooplankton communities of the African Great Lakes suggest that visual planktivory by fish is a dominant and persistent force in all the lakes. Moreover, it appears that in most of the lakes the intensity of the planktivory by fish is relaxed along an axis from inshore to offshore regions, to such an extent that invertebrate planktivory becomes a significant feature of the offshore environment. The exception to this pattern is Lake Tanganyika, where there is evidence that visual planktivory is great even in offshore waters. This exception is correlated with the presence of the endemic clupeid planktivores *Limnothrissa* and especially *Stolothrissa* in Lake Tanganyika. In lakes where transplants of one of these fish have occurred, striking and consistent changes in the resident zooplankton have followed. There is reason to believe that in the other lakes the indigenous zooplanktivorous fish, which are principally members of the families Cyprinidae and Cichlidae, are prevented by life history or physiology from exploiting the vast pelagic regions (Hecky 1984b; Turner 1982).

## COMPARATIVE FOOD WEB COMPOSITION

Plankton and fish communities characterizing pelagic regions of the African Great Lakes are compared in Table 1. The categories are constructed to represent biological elements that recur consistently among basins. The family Centropomidae includes species of *Lates*, including the Nile perch, which are important piscivores in many of the lakes. Planktivorous fish include members of the Cyprinidae (*Neobola*, *Rastrineobola*, *Engraulicypris*) and Characidae (*Alestes*) which have been reported to be important pelagic zooplanktivores, although in many cases life history may make these taxa more common in inshore than offshore areas.

The category for prawns includes freshwater shrimp (Decapoda) from both the Atyidae (*Caridina*, *Limnocaridina*) and Palaemonidae (*Macrobrachium*). These taxa have been characterized as epibenthic detritivores, but some are known to be nocturnally planktonic. It is difficult to conceive why a strict detritivore would migrate upward from the detritus-rich benthos under cover of darkness. Rather, it seems possible that these animals may be facultative planktivores whose access to zooplankton prey is limited by risk of visual predation from fish. Additional study of their trophic interactions would be desirable.

The only freshwater Diptera present in the pelagic region are species of *Chaoborus*, which become meroplanktonic in the third and fourth instars (Macdonald 1956) and can be important invertebrate planktivores. The family Cyclopidae represents free-living cyclopoid copepods, including *Mesocyclops*, which is predatory in its subadult and adult stages, as well as smaller, herbivorous or omnivorous taxa: *Tropocyclops* and *Thermocyclops*. Calanoid

**Table 1.** Plankton and Fish Communities from Pelagic Regions of the East African Great Lakes

	Lake Albert	Lake Edward
Centropomidae	<i>Lates niloticus</i>	(absent)
Planktivorous fish	<i>Rastrineobola argentea</i> <i>Alestes</i>	<i>Rastrineobola argentea</i>
Prawns	<i>Caridina nilotica</i>	
Planktivorous Diptera	<i>Chaoborus</i>	<i>Chaoborus</i>
Cyclopidae	<i>Mesocyclops</i> <i>Thermocyclops</i> <i>schuurmanae</i>	<i>Mesocyclops</i>
Diaptomidae	(absent)	(absent)
Cladocera	<i>Daphnia lumholtzi</i> <i>Diaphanosoma excisum</i> <i>Ceriodaphnia reticulata</i> <i>Ceriodaphnia cornuta</i> <i>Moina micrura</i> (inshore)	<i>Daphnia lumholtzi monacha</i> <i>Diaphanosoma excisum</i> <i>Ceriodaphnia dubia</i> <i>Ceriodaphnia cornuta</i> <i>Moina micrura</i> (inshore)
Rotifera	few	few
Phytoplankton	Bacillariophyta Chlorophyta Chrysophyta	Cyanophyta Chlorophyta
Sources	Rzoska 1975 Green 1971 Hecky and Kling 1987	Green 1971 Beadle 1981 Eccles 1985 Hecky and Kling 1987
	Lake Malawi	Lake Tanganyika
Centropomidae	(absent)	<i>Lates angustifrons</i> <i>Lates mariae</i> <i>Lates microlepis</i> <i>Lates stappersi</i>
Planktivorous fish	<i>Engraulicypris sardella</i>	<i>Limnothrissa miodon</i> <i>Stolothrissa tanganicae</i>
Prawns	<i>Caridina nilotica</i> (inshore)	<i>Limnocaridina</i> spp.
Planktivorous Diptera	<i>Chaoborus</i>	(absent)
Cyclopidae	<i>Mesocyclops</i> <i>Thermocyclops neglectus</i>	<i>Mesocyclops</i>
Diaptomidae	<i>Tropodiatomus cunningtoni</i> <i>Thermodiatomus mixtus</i>	(absent)
Cladocera	<i>Bosmina longirostris</i> <i>Diaphanosoma excisum</i>	(absent)
Rotifera	rare ( $<10\text{ m}^{-3}$ )	few
Phytoplankton	Cyanophyta Chlorophyta Bacillariophyta	Cyanophyta Chlorophyta Bacillariophyta Chrysophyta Ciliata <i>Strombidium</i>
Sources	Twombly 1983 Hecky and Kling 1987 Fryer 1957	Coulter 1991 Beadle 1981 Hecky and Kling 1987

Table 1, cont'd

	Lake Turkana	Lake Victoria
Centropomidae	<i>Lates niloticus</i> <i>Lates longispinus</i>	<i>Lates niloticus</i>
Planktivorous fish	<i>Neobola stellae</i> <i>Alestes minutus</i>	<i>Rastrineobola argentea</i>
Prawns	<i>Caridina nilotica</i> <i>Macrobrachium niloticum</i>	<i>Caridina nilotica</i>
Planktivorous Diptera	(absent)	<i>Chaoborus</i>
Cyclopidae	<i>Mesocyclops</i> <i>Thermocyclops hyalinus</i>	<i>Mesocyclops</i> <i>Tropocyclops confinis</i> <i>Tropocyclops tenellus</i> <i>Thermocyclops neglectus</i> <i>Thermocyclops emini</i> <i>Thermocyclops incisus</i> <i>Thermocyclops oblongatus</i> <i>Th. schuurmanae</i>
Diaptomidae	<i>Tropodiaptomus banforanus</i>	<i>Thermodiaptomus galeboides</i> <i>Tropodiaptomus stuhlmanni</i>
Cladocera	<i>Moina brachiata</i> <i>Moina micrura</i> <i>Diaphanosoma excisum</i> <i>Ceriodaphnia cornuta</i> <i>Daphnia barbata</i>	<i>Daphnia lumholtzi</i> <i>Daphnia longispina</i> <i>Diaphanosoma excisum</i> <i>Ceriodaphnia dubia</i> <i>Ceriodaphnia cornuta</i> <i>Bosmina longirostris</i> <i>Moina micrura</i>
Rotifera		few
Phytoplankton	Cyanophyta	Cyanophyta
Sources	Beadle 1981 Eccles 1985 Ferguson 1978	Green 1971 Rzoska 1957 Beadle 1981 Mwebaza-Ndawula 1994a Mwebaza-Ndawula 1994b
	Lake Kivu (1950s)	Lake Kivu (1980s)
Centropomidae	(absent)	(absent)
Planktivorous fish	(absent)	<i>Limnothrissa miodon</i>
Prawns		
Planktivorous Diptera	(absent)	(absent)
Cyclopidae	<i>Mesocyclops</i> <i>Thermocyclops consimilis</i> <i>Tropocyclops confinis</i>	<i>Mesocyclops</i> <i>Thermocyclops consimilis</i>
Diaptomidae	(absent)	(absent)
Cladocera	<i>Daphnia curvirostris</i> <i>Diaphanosoma excisum</i> <i>Ceriodaphnia cornuta</i> <i>Moina micrura</i>	<i>Diaphanosoma excisum</i>
Rotifera	few	few
Phytoplankton		Cyanophyta Chlorophyta
Sources	Dumont 1986	Dumont 1986 Hecky and Kling 1987



copepods are represented in some lakes by the family Diaptomidae, including the genera *Tropodiaptomus* and *Thermodiaptomus*. Cladoceran zooplankton include the herbivorous genera *Daphnia*, *Diaphanosoma*, *Ceriodaphnia*, *Moina*, and *Bosmina*. No predatory Cladocera have been reported from these lakes.

The dominant phytoplankton in the African Great Lakes are principally members of the algal divisions Cyanophyta (bluegreen cyanobacteria), Chlorophyta (green algae), Bacillariophyta (diatoms), and in a few cases, Chrysophyta (golden-brown algae). Cryptophytes and dinoflagellates, although present, are not conspicuous in terms of biomass (Hecky and Kling 1987).

Missing from Table 1 is reference to the freshwater jellyfish (*Limnocoidea*), of which species are known from both Tanganyika and Victoria (Coulter 1991; Beadle 1981). Although the medusae are capable of asexual reproduction by budding, and thus can develop populations independently of the littoral benthic polyp stage, the abundance and ecological significance of the taxa to the pelagic ecosystems of these lakes have not been well characterized, and so the potential importance of these jellyfish as invertebrate predators is not known at present.

Hecky (1984b) has attempted to summarize the relative magnitudes of primary production, zooplanktonic secondary production, and fish production from each of the lakes, and no substantial improvement over his effort is possible yet. Accurate, reproducible data are virtually nonexistent for zooplankton biomass and rates of production in the East African Great Lakes. In some cases where mesh sizes of plankton collections were specified (e.g., Worthington 1931 for Lake Victoria; Burgis 1984 for Lake Tanganyika) it is clear that quantitatively important elements of the fauna may have been missed. In other cases, the mesh sizes and construction of the sampling devices was not specified (e.g., Rzoska 1957, 1975; Green 1967a, 1971), and thus the observations cannot be repeated and compared.

### CHAOBORUS DISTRIBUTION

One analysis that can be conducted with Table 1 is to observe taxonomic categories that are missing from some lakes, but which are present in others. A particularly intriguing element in this regard is the invertebrate planktivore *Chaoborus*. The predator is present in Albert, Edward, Malawi, and Victoria, but is absent from Kivu, Tanganyika, and Turkana. Together with members of the obligately benthic Chironomidae, *Chaoborus* is responsible for spectacular synchronized emergences of lake flies, sometimes at densities of thousands per square meter (Macdonald 1953, 1956). Possessing a winged adult stage, it has ample potential to disperse and to colonize suitable habitats. Overlapping cohorts of *Chaoborus* exist at African lake temperatures, with individual generation times of two months (Macdonald 1956). Eggs deposited at the water surface sink to the sediments and hatch within two to four days. Both first and second larval instars are holoplanktonic for about two weeks, but in the third and fourth instars, the larvae burrow in the mud during day and rise into the water column to forage only at night, similar to the behavior of most temperate chaoborids. At the end of two months, larvae in their fourth instar pupate and emerge from the water as adult midges. Daytime burial in benthic sediments seems to be a behavior evolved to evade visual planktivory, and is not obligatory for all chaoborids. In fishless temperate lakes, for instance, the large *Chaoborus americanus* remains holoplanktonic, but it is extirpated when fish are introduced (Northcote et al. 1978).

At Lake Malawi, the winged adults of *Chaoborus edulis* are collected as human food, and chemical analyses of congeners from Lake Victoria confirm their nutritional value (Okedi

**Table 2.** Presence or Absence of *Chaoborus* in East African Great Lakes Ranked by Reported Conductivities, or Ranges of Reported Conductivities of Their Surface Waters

Lake	Conductivity ( $\mu\text{S}$ )	<i>Chaoborus</i>
Victoria	97–187	+
Malawi	210	+
Tanganyika	610–649	–
Edward	456–925	+
Albert	691–735	+
Kivu	1110–1240	–
Turkana	3000	–

Data from Talling and Talling 1965; Kilham 1971; Eccles 1985.

1992). Nonetheless, *Chaoborus* which pupate and emerge as winged, aerial adults have been regarded as lost potential productivity for the fishery of the lake (Turner 1982).

As an aquatic Dipteran, *Chaoborus* seems to have physiological constraints on its range of suitable habitats. Eccles (1985) suggested that its absence from Kivu, Tanganyika, and Turkana might be caused by the elevated salinities of those three lakes. As Table 2 demonstrates, however, Lakes Albert and Edward both possess higher conductivities than does Tanganyika, even though *Chaoborus* abounds in both of the former systems. There is precedent, however, for believing that plankton species distributions may be affected by total dissolved ion concentrations. LaBarbara and Kilham (1974) demonstrated chemical segregations of African copepod taxa by lake water conductivities. In temperate saline lakes, *Chaoborus* is restricted to salinities of 3–10 per mille (Topping 1971; Hammer 1986). Even more telling, however, is the fact that solute concentrations tolerated by aquatic Dipteran larvae are a function of water temperature (Hammer 1986, p. 429). At cold hypolimnetic temperatures in temperate lakes (5°C), the larvae can tolerate much higher salinities than they can bear at warm temperatures (20°C). It thus appears that experimental work is needed on the salinity tolerances of African chaoborids at ambient lake temperatures (>22°C) in order to determine the role of lake chemistry in distribution patterns.

There is another factor related to the life history of *Chaoborus* that must be considered, moreover, to understand why it is excluded from some lake environments. The larvae are tactile, sit-and-wait predators with limited escape responses. Once observed by a mobile, visual predator, they have little chance of survival. Eggs deposited by adult females at the lake surface settle to the mud and hatch, and subsequently 75% of the larval life cycle (instars 3 and 4) is spent at depth or among the sediments during daylight hours. Lakes which have small proportions of their sediment surface available as suitable habitat for the larvae, or where steep submarine topography affords poor sediment refuge, may present insurmountable challenges to successful establishment of meroplanktonic chaoborid populations. Of the African Great Lakes, both Kivu and Tanganyika have the smallest proportions of their benthic areas exposed to aerobic waters, even during full circulation (Table 3). Larval *Chaoborus* have physiological mechanisms to withstand temporary anoxia, but prolonged anaerobic existence at elevated temperatures has not been reported, and the larvae may be

**Table 3.** Morphometry of East African Great Lakes ( $A_{ox}$  = maximum area of bottom sediments oxygenated during full circulation;  $z_{max}$  = maximum depth;  $z$  = mean depth)

Lake	$A_0$ (km <sup>2</sup> )	$z_{max}$	$z$	$A_{ox}$ (%)
Albert	6800	58	25	100
Edward	2325	117	40	95
Kivu	2370	485	240	20
Malawi	28800	704	290	45
Tanganyika	32600	1470	580	20
Victoria	68800	84	40	100
Turkana	7560	120		100

Data from Hecky and Kling 1987; Marshall 1991; Beadle 1981; Hecky and Bugenyi 1992; Talling 1965.

incapable of surviving those conditions. Consequently, planktivory by littoral fish communities alone could prove devastating in lakes where habitat is restricted to a littoral fringe. The extent to which deep, aphotic lake regions can serve as a refuge from visual planktivory is unknown at present.

## ROTIFERA

Another striking feature of Table 1 is the fact that rotifers are rare in all African Great Lakes pelagic environments. Scarcity of these animals seems to be a particular feature of the large, deep lakes because shallow lakes like George and Kyoga have much higher abundances and species richness of rotifer taxa (Table 4). Individual body masses of rotifers are typically at least two orders of magnitude less than those of individual crustacean zooplankton (Bottrell et al. 1976). Consequently, by comparison with other plankton groups, the rotifers represent a trivial proportion of zooplankton biomass in these large lakes.

Rotifers tend to be more species rich and abundant in African rivers and lake littoral regions than in the open waters of East Africa (Green 1967b). Highest rotifer abundances may occur in saline, soda lakes which have an otherwise restricted planktonic fauna (Nogrady 1983). Rotifers are susceptible to invertebrate planktivory, especially from cyclopoid copepods (Stemberger and Gilbert 1987) and early instar *Chaoborus* (Neill and Peacock 1980). Their life history characteristics, including cyclic parthenogenesis and the interesting phenomenon of eutely, or cell constancy, permit them to exhibit short maturation times (hours) and very rapid rates of population growth under suitable environmental conditions (Bennett and Borass 1989). When these opportunistic organisms are consistently scarce, and the requisite predators are abundant, as in pelagic regions of the African Great Lakes, biological control of their distributions through invertebrate predation should be suspected. Unlike in temperate lakes, where predator populations wax and wane seasonally, rotifers have no seasonal refugium in the endless summer of East African lakes.



**Table 4.** Comparative Numerical Inventories of Planktonic Cladocera and Rotifera in Large East African Lakes

Lake	Station depth (m)	Cladocera		Rotifera	
		Indiv m <sup>-2</sup>	Species	Indiv m <sup>-2</sup>	Species
Albert (midlake)	47	160000	6	370	5
Edward (offshore)	24–30	60000–220000	5	620–1300	5
George	2–4	1400–10000	3	6800–25000	15
Kyoga	4–6	960–8600	13	2500–14000	24
Malawi	>50	50000–600000	2	<500	na
Tanganyika	>50	0	0	"rare"	na
Victoria	28	37000	9	3000	9

Data rounded to two significant digits from Green 1967a, 1967b, 1971; Twombly 1983; Coulter 1991.

## CLADOCERA

The distribution of Cladoceran taxa in the African Great Lakes shows instructive complements to that of the Rotifera. Green (1967a, 1971) assembled an illuminating collection of data from the large lakes that drain to the White Nile. His data and interpretations argue convincingly that planktivory by fish is concentrated in the nearshore regions of the large lakes, especially Albert, Edward, and Victoria, and that the intensity of visual planktivory decreases toward offshore waters. He demonstrated the pattern with a series of species transitions. In both Lake Albert and Lake Edward, for instance, a large-bodied, conspicuous herbivore, *Daphnia lumholtzi* var. *monacha*, was present in highest abundance at midlake stations. The taxon was common in the stomachs of plantivorous fish, and its population abundance decreased rapidly near shore where planktivorous fish were present. Near shore in Lake Albert, the large bodied *Daphnia* was replaced by a smaller bodied, helmeted form, *Daphnia lumholtzi* (typical form), and by other small Cladocera. Similarly, within the genus *Ceriodaphnia*, the larger form *C. dubia* was present offshore, and the smaller bodied species *C. cornuta* was present inshore.

Green (1971) demonstrated that the larger Cladoceran taxa also had larger, more pigmented eyes, and thus by analogy with Zaret's (1969, 1972) evidence, they would be more visible to planktivorous fish. Abundances of Cladocera in the offshore waters of deep lakes compared with the shallow lakes George and Kyoga (Table 4) suggest that the Cladocera experience a refuge from fish planktivory offshore.

Green (1967a, 1971) sought to explain the success of large bodied Cladocera in offshore lake waters by the conventional theory of the time: the size–efficiency hypothesis of Brooks and Dodson (1965). He regarded the large animals to be competitively superior to the small ones, and thus better able to dominate when compensatory predation was removed. However, he offered no evidence about relative rates of fecundity, resource depletion, or growth efficiency that would be essential to establish a competitive interaction. Instead, the patterns he reports are tantalizingly consistent with the notion that whereas vertebrate planktivory wanes from inshore to offshore, the strength of invertebrate planktivory does the opposite.

**Table 5.** Lake Victoria Zooplankton: Comparison Between Inshore (Pilkington Bay, 10 m) and Offshore (NE open Lake Victoria, 67 m) Communities, 1956 (data from Rzoska 1957)

Taxon	Percent by count	
	Inshore	Offshore
<i>Moina</i>	27	5
<i>Tropocyclops</i>	8	0
<i>Daphnia lumholtzi</i>	0.4	0
<i>Bosmina longirostris</i>	2	1
<i>Diaptomus</i>	33	25
<i>Thermocyclops</i>	7	22
<i>Mesocyclops</i>	4	12
<i>Diaphanosoma</i>	3	5
<i>Ceriodaphnia cornuta</i>	2	8
<i>Ceriodaphnia dubia</i>	0	4
<i>Daphnia longispina</i>	0	5

Because invertebrate predators are typically smaller with respect to their prey than are fish, the invertebrates are subject to gape-limitation, *sensu* Zaret (1980). Their prey can find refuge in large body size such that capture and handling become ineffective (Kerfoot 1977a, 1977b). The larger bodied Cladocera present in the offshore waters of Albert, Edward, and Victoria would be less susceptible to predatory cyclopoids and diptera than would their smaller congeners. A particularly good example can be found in the genus *Ceriodaphnia*, involving the species *C. cornuta* and *C. dubia*.

*C. dubia* is an animal of larger body size than *C. cornuta*, and it is a characteristic species in the offshore waters of Lakes Albert, Edward, and Victoria (Green 1971; Rzoska 1957) (see Table 5). Specimens of *C. cornuta* from offshore regions tend to be of a morphological variety that has been called *C. rigaudi*, which is larger in body dimensions than is the typical form. Zaret (1969, 1972) studied these two forms, which also occurred in Gatun Lake, Panama, and demonstrated that visual predation by planktivorous fish was based mainly on the size of the conspicuous, pigmented eye. By this logic, more conspicuous animals would experience differential mortality and be excluded from habitats that possessed high concentrations of planktivorous fish. Green (1971) demonstrated that for the African lakes, eye-size is well correlated with body size. That explains the absence of larger forms from nearshore waters. But what prevents the smaller forms from being successful offshore? As with the rotifers, the likely answer is mortality imposed by abundant invertebrate predators, particularly *Mesocyclops*.

## THE APPARENT INCONGRUITY OF LAKE TANGANYIKA

Based on the circumstantial evidence assembled, it appears that most of the Great Lakes of East Africa have food webs that are influenced most strongly by fish planktivory nearshore

and by invertebrate planktivory offshore. Lake Tanganyika presents a contradiction to this pattern. No Cladocera are present in the offshore plankton of the lake, although some species of Chydoridae are found inshore and in adjoining waters (Coulter 1991). Moreover, there is evidence that the trend in vertebrate planktivory is opposite in Lake Tanganyika from that of the other lakes.

Mashiko et al. (1991) present demographic data contrasting lagoon and lake populations of the endemic shrimp *Caridina tanganyicae*. They demonstrate that lake animals are on average much smaller than those of the inshore lagoon. Lake populations mature at smaller body sizes than do lagoon populations, even though each population seems to invest similar fractions of total body mass in reproductive effort. Because there was no significant difference in reproductive effort scaled to body size between the populations, it seems less likely that the differences are caused by food limitation than that the lake populations are subject to more intense size-selective predation.

The critical, anomalous feature of Lake Tanganyika with respect to the other lakes is the presence of two endemic freshwater sardines, *Limnothrissa* and *Stolothrissa*, derived from marine stocks that successfully invaded rivers of West Africa and subsequently became established in Lake Tanganyika through the Zaire drainage (Coulter 1991). The fish are derived from effective oceanic planktivores, and one of them, *Stolothrissa*, is entirely pelagic, spawning and living its entire life away from shore. No comparable species exist in the other African Great Lakes, except now in Kivu where *Limnothrissa* was intentionally introduced. Before introduction of the planktivore, zooplankton biomass has been roughly  $7.5 \text{ g DW m}^{-2}$ , but subsequent to establishment of *Limnothrissa*, Dumont (1986) found only  $0.15 \text{ g DW m}^{-2}$  in a single, expeditionary sample. A similar experience was reported for Lake Kariba, an artificial impoundment, which was stocked with *Limnothrissa*. Both abundances and species richness of Cladocera were reduced, and *Chaoborus* was eliminated (Marshall 1991). A pattern of progressive reduction and elimination of zooplankton populations according to their body size in the face of visual planktivory was similarly documented by Gliwicz (1985) for Cahora Bassa, a reservoir downstream from Kariba that became colonized by *Limnothrissa*, as well. The case studies of species introduction to Lakes Kivu, Kariba, and Cahora Bassa constitute quasi-experiments at the whole ecosystem level that are consistent with intense offshore vertebrate planktivory by clupeoid fishes in Lake Tanganyika. There is no analog to these offshore planktivores in the other Great Lakes, where native freshwater Cyprinidae and Characidae exploit the plankton. The implications of the clupeoid stocks in Tanganyika for the anomalously high pelagic fishery potential of the lake have been discussed by many authors (Hecky et al. 1981; Hecky 1984b; Hecky 1991; Coulter 1991).

## FOOD WEB DYNAMICS IN LAKE VICTORIA

Recent changes in the food web of Lake Victoria represent another case that deserves special attention, because the changes offer insight to trophic dynamics in large tropical pelagic ecosystems. Lake Victoria and its watershed have been transformed by events of the past century. The transformations have included loss of forests, lake eutrophication, deep water deoxygenation, and changing water levels, algal species, mixing dynamics and productivity. Understanding the processes that brought about these conditions is an essential first step in reconstructing the long histories of the African lakes, because the changes which occurred in Victoria may have pre-human analogs in the sedimentary stratigraphic records from the East African lakes. In fact, the most powerful way to test the validity of inferences about

lake history is to examine systems that have been perturbed in a defined way, follow the perturbation signals through the ecosystem, and document their traces in the stratigraphic record.

The condition of Lake Victoria has changed profoundly during the last three decades. Talling (1966) reported a flora rich in large diatoms, particularly *Melosira* and *Stephanodiscus* in 1960 and 1961, with offshore Chl *a* ranging from 1.2 to 5.5 mg m<sup>-3</sup> in the euphotic zone, SRSi generally between 67 and 75 µM (4.0–4.5 mg/l SiO<sub>2</sub>), and O<sub>2</sub> extending to the deep sediments offshore. In contrast, the lake is now dominated by cyanobacteria, biomass is elevated, surface SRSi has declined, and deep waters are regularly anoxic (Hecky 1993).

Another conspicuous change to the Lake Victoria ecosystem has been the alteration of its fish community. During the 1980s, the fishery of the lake underwent radical transformation by the success of introduced species of the Nilotic fauna, in particular *Lates niloticus* (Nile perch, a piscivore) and *Oreochromis niloticus* (Nile tilapia, an herbivore). Vast endemic species flocks of haplochromine cichlids declined as the introduced species became established (Ogutu-Obwayo 1990a, 1990b, 1992; Ligtvoet and Witte 1991; Witte et al. 1992a, 1992b). These species were introduced to the lake in the 1950s, but they did not become common or widespread for nearly two decades; by the late 1980s they dominated the fish catch to near exclusion of all native species except for *Rastrineobola argentea* (Ogutu-Obwayo 1990b).

Introduction and success of the nilotic species followed an episode of nearly unregulated reduction of gill net mesh sizes and collapse of the traditional tilapia fisheries, and was contemporaneous with initiation of commercial trawling for demersal haplochromines. The haplochromine stocks of Lake Victoria had been regarded as one of the great examples of vertebrate species radiation on the planet, with at least 300 species (van Oijen et al. 1984). Small clutch sizes and mouth breeding behaviors of the haplochromines are inconsistent with high rates of exploitation by either overfishing or predation. The only native species of Lake Victoria which has increased in yield during recent years is the small pelagic cyprinid, *Rastrineobola argentea*. This species had been common during the earliest surveys of the lake (Graham 1929, Worthington 1929), and it is not clear if present yields faithfully represent increased populations, or if they merely reflect higher fishing pressure on existing stocks.

The cause for the sweeping changes in physical, chemical, and biological properties of the lake is not known, because limnological observations were interrupted. As a result, the condition of Lake Victoria presents a forensic challenge to limnological theory, and three main competing hypotheses have been advanced to explain the changes (Hecky 1993). Lake productivity mechanisms may have changed as a result of the introduced piscivore and the ensuing food web changes. Alternatively, increased nutrients may be entering the lake from atmospheric precipitation, or watershed runoff, or both. Finally, there may also have been changes in the internal nutrient recycling mechanisms of the lake. Changes in regional climate, which caused changes in lake level, may have produced altered patterns of physical mixing and thermal stratification, which in turn influenced the development of diazotrophic cyanobacteria, hypolimnetic deoxygenation and altered sedimentary nutrient exchange.

Lake Victoria is the shallowest of the East African Great Lakes (80 m maximum depth), but it has the largest surface area of any freshwater lake other than Superior. Although its basin is ancient, the lake has endured marked changes in volume which have influenced the development of its fauna. During the late Pleistocene the lake was greatly reduced in area, more saline than today, and perhaps completely dry (Kendall 1969; Stager 1984; Stager et



al. 1986). In very recent times the lake has responded to climate variation by significant increases in lake level, first in the early to mid 1960s and then again in the late 1970s (Kite 1981; Piper et al. 1986). Today its flushing time (volume/outflow) is 140 yr (Hecky and Bugenyi 1992), and its water budget is dominated by rainfall. The long flushing time means that nutrient retention is high, and it also means that the lake would recover slowly from chemical alterations. The annual cycle of nutrients in surface waters in Victoria, as in the other Great Lakes of East Africa, is believed to be controlled by vertical mixing and stratification (Hecky and Kling 1987). Victoria is one of the few lakes in Africa for which historical data are available about annual cycles of stratification, nutrient concentrations, and productivity (Talling 1965, 1966).

Over the period of the transformation of its fishery, silicon concentrations of Lake Victoria declined by an order of magnitude (Hecky and Bugenyi 1992). Sulfate concentrations appear to have declined as well, but Hecky and Bugenyi (1992) suspect that the apparent differences are possibly the result of more specific and more accurate modern methods (ion chromatography). The concentrations are probably the lowest of any large water body on earth. Moreover, residence time of  $\text{SO}_4$  in the water column of Lake Victoria is less than 2 months based on rates of allochthonous income and water column inventories (Hecky and Bugenyi 1992), which supports Beauchamp's (1953) suggestion that it is behaving as a nutrient. Lehman and Branstrator (1994) have recently confirmed that turnover rates of sulfate are two weeks or less in the water column, and that the flux is dominated by biological uptake into algal particles larger than  $1\text{ }\mu\text{m}$ . Despite the essential role of sulfate as a nutrient in Lake Victoria, however, the compound is not scarce enough to limit either uptake kinetics or biomass yields, and hence it may serve as a good biological tracer in the lake.

The decrease in Si in Lake Victoria is even more extreme than that observed in the Laurentian Great Lakes during their eutrophication (Schelske 1988). In the Laurentian lakes, increased phosphorus loading was believed to increase biomass and to cause increased algal demand for Si. In Lake Victoria, offshore TP concentrations have remained constant or slightly increased from 1961 to the present, although even in 1961  $\text{PO}_4$  concentrations were in excess of algal demand and unlikely to limit phytoplankton growth in the offshore (Talling 1966). Modern nutrient bioassay experiments have confirmed that P addition to lake water does not increase algal biomass (Lehman and Branstrator 1993), and that offshore concentrations of  $\text{PO}_4$  are in excess of algal half saturation constants for uptake rates (Lehman and Branstrator 1994). Nearshore, concentrations of  $\text{PO}_4$  are much reduced, and turnover times for the ambient dissolved pools which are as high as 5 days offshore decline to 5 min in the nearshore environment (Lehman and Branstrator 1994). The net result is that when water exits Lake Victoria as the White Nile, SRP concentrations are near zero, compared with  $1\text{ }\mu\text{M}$  or more offshore, which means that on a lakewide, ecosystem basis virtually all inorganic P supplied to the lake is converted to organic matter (Hecky 1993). This is evidently not a new situation for the lake, because Talling (1966) reported depressed concentrations of both  $\text{SRSi}$  and SRP at his northern inshore stations compared with offshore waters of the lake.

Nitrogen had been considered the macronutrient most likely to limit phytoplankton growth in Victoria (Talling and Talling 1965), based on low nitrate concentrations ( $<1\text{ }\mu\text{M}$ ); modern bioassay experiments confirm that additions of inorganic nitrogen can increase algal biomass (Lehman and Branstrator 1993, 1994). There is also evidence that elevated algal



biomass in recent years has reduced the vertical extent of light penetration, and that rates of photosynthesis show signs of light limitation (Mugidde 1993).

If the changes to Lake Victoria have been caused by nutrient addition (eutrophication), the observed increase in chlorophyll and algal biomass would have to be accompanied by increased supplies of nitrogen, because water column reserves of the element are small and incapable of supporting large biomass increases. Estimated export of N from catchment to lake is more than two orders of magnitude smaller than the flux required by measured rates of primary production (Lehman and Branstrator 1993). Internal sources of N are unlikely to make up the difference because sediments and overlying water are probably a sink rather than a source of inorganic N, owing to denitrification (Hecky 1993). Nitrate concentrations in rainwater are similarly insufficient (Talling 1966; Lehman and Branstrator 1993).

The other major source of N is elemental, atmospheric  $N_2$ . The algal community of Lake Victoria is now rich in cyanobacteria (Ochumba and Kibaara 1989; Ochumba 1990), including many diazotrophic forms (Hecky 1993). It is not yet known how much of the production is based on "new" nutrients rather than recycled ones, but clearly sedimentary fluxes, denitrification losses, and the increased algal biomass from historical levels must be balanced by accelerated N-fixation, because watershed inputs and precipitation account for a trivial fraction of algal demand for N. Hecky (1993) measured substantial rates of N-fixation and also showed that excess SRP offshore was converted to particulate, algal P inshore as N was added to the system through N-fixation. Stoichiometry of the particulate material inshore indicated possible P deficiency.

From observations about the P economy of the lake, it appears that despite the proximate roles of light and N limitation, the master controlling nutrient for Lake Victoria may be P. In the long term, and on the basin-scale, N-fixation during the "endless summer" causes all excess  $PO_4$  to be used in biological processes.

An alternative hypothesis emphasizes the altered trophic structure of Lake Victoria after the introduction of nilotic fish species (Witte et al. 1992a; Baskin 1992). Many of the haplochromine species eliminated from the fauna had been primary and secondary consumers. If these food web changes, tied to success by an introduced piscivore, had reduced herbivory and detritivory by haplochromines, and had thereby increased sedimentation of organic matter, then some of the observed changes might result from a trophic cascade, *sensu* Carpenter et al. (1985). For instance, decreased herbivory by haplochromines directly on algae might permit increased algal biomass as well as increased rates of organic matter export from euphotic zone to sediments. The increased vertical particulate fluxes might lead to increased sediment oxygen demand, decreased hypolimnetic oxygen concentrations, and lower rates of SRSi regeneration, owing to higher burial rates of diatom frustules.

The hypothesis of lake ecosystem change by trophic cascade, or "top-down" control, depends critically on the ability of Lake Victoria haplochromines to suppress the algae of the lake well below carrying capacity. The presumption must be that historically, as at present, diazotrophic cyanobacteria would have been able to fix enough atmospheric  $N_2$  to elevate algal biomass substantially, if only compensatory losses through herbivory were not so high. By this reasoning, the changes in nutrients and algal communities would have occurred contemporaneously with, or subsequently to, collapse of the haplochromine stocks, which is known to have occurred during the early 1980s (Ogutu-Obwayo 1990a, 1990b, 1992; Kudhongania et al. 1992).

In contradiction to this second hypothesis, however, Hecky (1993) showed from paleolimnologic analyses that eutrophication by increased P loading and algal community change,

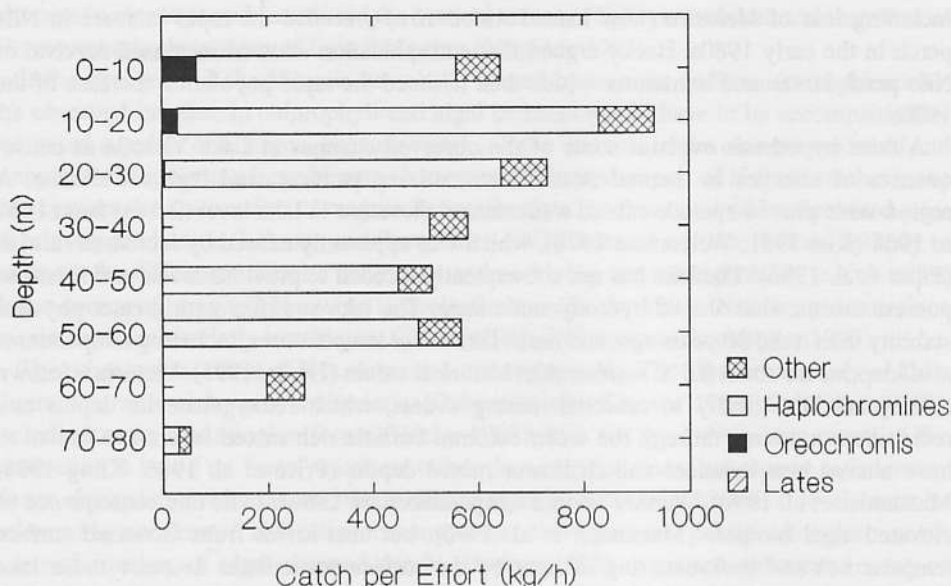
including loss of *Melosira* (now named *Aulocosira*) preceded the rapid increase in Nile perch in the early 1980s. Hecky argued that eutrophication allowed increased survival of Nile perch larvae and immatures which then initiated the rapid population increase of the 1980s.

A third hypothesis explains some of the observed changes in Lake Victoria as consequences of changes in thermal stratification, mixing patterns, and regional climate. A region-wide pluvial episode caused a substantial elevation in lake level (2.5 m) from 1961 to 1964 (Kite 1981; Welcomme 1970), which was apparently caused by increased rainfall (Piper et al. 1986). The lake has not subsequently receded to previous levels and seems to possess a somewhat altered hydrodynamic state. The lake stratifies with greater physical stability than it did 30 years ago, and mean lake water temperatures, including temperatures at all depths, are about 0.5°C warmer than historical values (Hecky 1993). Victoria is known to respond biologically to seasonal mixing events, which reoxygenate its depths and redistribute nutrients through the water column. Particle-rich mixed layers are known to have altered heat balances and shallower mixed depths (Price et al. 1986; Kling 1988; Mazumder et al. 1990). Warmer surface temperatures are known to be one consequence of elevated algal biomass (Mazumder et al. 1990), but heat losses from increased surface temperatures and backscattering of light by the surface particulates decrease mean lake temperature (e.g., Hecky 1984a). Hence, the increase in water temperatures at all depths is strong evidence of regional climate variation.

Prolonged and intensified stratification, or restricted vertical mixing, encourages the development of more extreme hypolimnetic oxygen deficits, and decreased rates of vertical diffusive flux of SRSi to surface waters (Lehman and Branstrator 1993). Light limitation is important in optically deep lakes like Victoria, where diel mixing can suspend algae for substantial periods below the euphotic zone. In such lakes, more stable water columns permit the establishment of surface populations of diazotrophic cyanobacteria (Reynolds 1984), which rely on light energy for both N-fixation and C-fixation. Thus, increased thermal stability provides a mechanism for positive biotic feedback on the nitrogen cycle, and for the fact that present levels of algal biomass are from 2- to 10-fold higher offshore than 30 years ago (Talling 1966; Mugidde 1993).

By reason of either the first (eutrophication) or third (climate change) hypothesis, the changes at higher trophic levels could have been in part consequences of the nutrient and stability changes. Benthic trawl surveys (Bergstrand and Cordone 1971; Kudhongania 1973; Kudhongania and Cordone 1974) had documented the widespread distribution of haplochromines at all lake depths, although abundances were somewhat reduced in the deepest strata (Fig. 1), where Talling (1966) had reported seasonal O<sub>2</sub> depression. Nile perch, which had been introduced a decade earlier, were extremely rare and confined to littoral depths. If widespread deoxygenation of hypolimnetic regions during the 1970s had led to loss of haplochromine habitat and dispersal of demersal stocks, those displaced fishes may have provided an important resource to the Nile perch, and thereby stimulated their population explosion in the 1980s (Hecky 1993).

Changes in the recent paleostratigraphy of Lake Victoria sediments lend support to the view that lower food web events preceded the transformation of the fishery. Hecky (1993) demonstrated that *Melosira* species, which had formerly been common, declined precipitously shortly after 1960. *M. nyassensis*, in particular, is a heavily silicified species that grows best during periods of very deep, intense mixing, which delivers cells to the euphotic zone (Kilham et al. 1986). During 1960–61 (Talling 1966), this species developed popula-



**Figure 1.** Fish distributions in Lake Victoria assessed by lakewide benthic trawl surveys, 1969-71, previous to major food web changes. Note the decreased abundances in the deepest strata. Data from Kudhonganika (1973).

tions during strong mixing to 60 m. The species has been virtually absent in recent years. The contracted euphotic zone (Mugidde 1993, Hecky 1993) now contains many cyanobacteria, some of which are diazotrophic and thereby contributors to the nitrogen budget.

There is strong evidence that real changes have occurred to the mixing regime of Lake Victoria during this century, and the paleolimnological evidence indicates that the changes may have some temporal correlation with the changing lake levels and the conditions that produced them. The hypothesis that alteration of Lake Victoria was caused by a trophic cascade from piscivory triggered by introduction of the Nile perch appears untenable based on the temporal sequence of events. The increased algal biomass and lowered oxygen concentrations of Lake Victoria are a source of concern about the trajectory and future state of the lake. They imply there is an increased oxygen demand in the lake's deep water, or that oxygen levels are being recharged less effectively. Reduced oxygen levels lead to decreased hypolimnetic volume habitable by fish during seasonal stratification, and the loss of habitat most likely leads to loss of species and lower potential fishery yield.

Lake Victoria offers a compelling challenge to paleolimnology because the ecosystem changes of the last 30 years have been wholesale and dramatic (Hecky 1993). The record of these changes is now held in the sediments, and it is the study of recent lake history which may ultimately resolve among the competing hypotheses, as well as provide a modern calibration for interpreting more ancient records of change buried in the sediments. Many of the sedimentary changes, including loss of *Melosira* and rise of *Cyclostephanos* have analogs in the records of the other great lakes, such as Kivu and Tanganyika (Haberyan and Hecky 1987).

## SUMMARY AND RESEARCH CHALLENGES

The Great Lakes of East Africa contain food webs that are characterized by strong interactions among organisms and between biota and geochemical processes. These biological interactions seem to be forced by absence of seasonal time lags and temporal refugia from interaction. In some cases, environmental conditions and history have produced enormous species richness, as among cichlid fishes and gastropods of littoral and benthic regions. In pelagic regions, however, the food webs are simple by comparison with temperate pelagia, and biological interactions, particularly predation, seem to have a dominating influence.

As tempting as first glimpses of food webs in these lakes may be, knowledge about them is tentative, and must be improved and placed on a firm, quantitative base. Comparative biomass inventories of plankton communities by standard methods in the lakes are needed, as are seasonal and interannual estimates of primary and secondary production. Only by collecting such data will it become possible to measure fluxes of carbon and essential nutrients through major trophic pathways and among ecosystem components. Time series observational and experimental data about fauna and flora, physiological rates, and biogeochemical fluxes are essential, as well, in order to characterize present conditions and variabilities among lakes. In lakes where some faunal elements are missing (e.g., *Chaoborus*, Cladocera in Tanganyika), improved sampling and experimentation is called for in order to determine if taxa are unable to colonize the habitats, or are instead suppressed to low abundances by strong biological forces.

Finally, these lakes offer excellent opportunities to establish the linkages between modern ecosystem processes and recent sedimentary records. Some of them have experienced significant perturbations in recent time (Hecky 1993), and effects of environmental change are accelerating (Cohen, this volume). It will be important to establish the ways that modern changes are recorded in lake sediments in these basins in order to make the long and often excellent paleostratigraphies of many basins interpretable as a history of ecological and environmental change.

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